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FINAL TECHNICAL REPORT

MARINE BIOSURFACES RESEARCH PROGRAM

OFFICE OF NAVAL RESEARCH

CONTRACT NUMBER: N00014-87-K-0685

Full Title: HYDRODYNAMIC FACTORS CONTROLLING SETTLEMENT IN FOULING ORGANISMS

Abbreviated Title: HYDRODYNAMICS OF SETTLEMENT

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OBJECTIVES

In recent years considerable effort has been directed toward understanding the behavioral and physiological events leading to the settlement and recruitment of fouling organisms. A wide variety of animals express preferences in the sites where they settle in response to chemical cues and various physical aspects of the substratum. However, these preferences cannot be expressed if hydrodynamic factors prevent larvae from reaching and adhering to the substratum. Thus the expression of site preference can depend on the mechanics of settlement, and it seems likely that a thorough understanding of these mechanics will be useful in the manipulation and control of fouling on man-made structures.

Several studies have examined the effects of flow on settlement, but very few of these have examined the flow itself in spatial and temporal detail suffcient to determine the mechanism(s) of its effects. For example, there is a wealth of data available regarding the time-averaged boundary-layer flow over rough and smooth substrata, but this information is generally confined to unidirectional flow whereas real-world flows are often oscillatory, and data are not available regarding the flow field in the topographically complexmicrohabitats that fouling organisms often prefer. Even in those cases where sufficient detail is known about flow to enable its application to biological problems, the appropriate theoretical framework is often not available.

In response to this lack of detailed information about the effects of flow on settling organisms, this project had the following objectives:

(1) To model the effects of near-substratum turbulence on the rate of delivery of larvae and spores to the substratum.

(2) To quantify the instantaneous flow regime in and near settlement microhabitats subjected to wave-induced oscillatory flow.

(3) To explore the effects of this flow regime on the pattern of settlement of algal spores and zygotes, which lack the post-settlement behaviors that complicate the study of settling larvae.

(4) To quantify the adhesive tenacity of algal zygotes as a means of assessing their susceptibility to hydrodynamic disturbance.

METHODOLOGY

Model of Turbulent Delivery

The effects of near-substratum turbulence were modelled using a random walk, Monte Carlo approach to the diffusive transport of particles in the benthic boundary layer. The simplicity of this approach, coupled with the ease it offers in the formulation of boundary conditions, was deemed sufficient to outweigh the disadvantage of a relatively long computer run time.

The details of the method are described in Denny & Shibata (1989).

Measurement of Flow in Microhabitats

Settlement microhabitats were modelled using small (3-12 mm diameter, 3-6 mm deep) cylindrical "pits" in an otherwise flat substratum. Flow in these microhabitats was measured using a combination of three techniques:

(1) Field measurements were obtained by orienting the substratum horizontally at a depth of 3-5 m beneath the ocean's surface offshore of Hopkins Marine Station. A small photoresistor was held in place beneath a clear plastic window in the base of each microhabitat, and a blue dye solution (slightly negatively buoyant with respect to seawater) was slowly pumped into each pit. In the absence of flow, dye filled the pit, thereby reducing the light impinging on the photoresistor. The presence of mixing in the pit reduced the concentration of dye, an effect that was sensed as an increase in the intensity of light reaching the photoresistor. By calibrating each photoresistor for dye concentration, and knowing the rate at which dye entered the pit, instantaneous measurements of light intensity could be used to quantify the rate at which water in a microhabitat was exchanged with water outside. Measurements of this type were conducted simultaneously on 4 pits (a fifth pit served as a control for ambient light level), and were accompanied by measurement of the mainstream flow over the substratum and of local hydrostatic pressure (a measure of wave amplitude). Similar measurements of

microhabitat mixing were made in a laboratory flume that provided oscillating flow with a period of 7.7 s and a velocity amplitude of up to 1.1 m/s.

(2) In addition to aiding in the measurement of mixing, the oscillatory-flow flume allowed us to visualize the pattern of flow in each microhabitat. A telemicroscope poised above the flume's working section and over the substratum was used to project an image of the pit and its enclosed dye onto a video camera, and the subsequent video recordings were analyzed frame-by-frame.

(3) An acoustic Doppler flow meter (University of Iowa 545C) was used in the flume to quantify the small-scale velocity field within the microhabitats. A field-portable version of this flowmeter was designed and built, but the inconsistent nature of acoustic scattering particles in ambient seawater precluded its practical use.

Together these three approaches provided a detailed picture of the flow in the type of microhabitat preferred by many settling organisms.

Measurement of Adhesive Tenacity

The ability of algal zygotes to adhere to the substratum in the face of imposed flow was measured in a specially-designed flume. This consisted of parallel flat plates (approximately 10 cm X 30 cm) spaced 2.8 mm apart. Water was forced to flow between these plates, thereby creating a parabolic velocity gradient

within the flume's working section. By varying the volumetric flow rate into the flume, the steepness of this velocity gradient (and thereby the shear stress on the flume walls) could be regulated. The narrow gap between plates ensured that flow remained laminar to quite high velocities, allowing for easy calculation of the boundary shear stress imposed on algal zygotes attached to the plates. The ability of organisms to adhere to the plates was observed through a dissecting microscope, and each experiment was video recorded for later analysis.

Zygotes of the rockweed *Pelvetia fastigiata* were shed onto the dry flume substratum and allowed to adhere for varying periods. This procedure mimics that found in nature where zygotes are shed at low tide. The ability of zygotes to withstand imposed shear was subsequntly quantified as a function of the time allowed for adhesion.

Field Measurement of Settlement Patterns

To explore the effects of flow in defined microhabitats, settlement plates were constructed in which pits were drilled with dimensions corresponding to those used in the measurements described above. Each PVC plate was carefully aged in seawater and cleaned to avoid any toxic effects on settling spores and was then placed in the field. The surface plane of each plate was held vertical to avoid problems of sedimentation. After a period of 2-7 days plates were retrieved and the location of algal spores in and near each microhabitat was censused.

RESULTS

Models of Turbulent Delivery

Although the intense turbulence found in the benthic boundary layer over wave-swept objects is likely to negate the ability of settling larvae to choose actively the site at which they first contact the substratum, this same turbulence ensures that the near-substratum flow field is so effectively mixed that larvae are reliably delivered to the substratum (Denny & Shibata 1989). Further, once larvae have been once brought into contact with the substratum, the diffusive nature of turbulent flow makes it likely that they will thoroughly "explore" a small area of the substratum before being wafted off to a distant area. This effect is enhanced by the relatively slow exchange between water within microhabitats and the mainstream flow (see below). Thus, the presence of microhabitats serve to retain larvae in the vicinity of their first contact with the substratum. A more thorough discussion of these results, including speculation as to the role of swimming speed and substratum rugosity, can be found in Denny & Shibata (1989) and Denny & Humphrey (1989). Note that effective delivery of larvae to a substratum does not imply that larvae, once delivered, are able to adhere.

Flow In Microhabitats

Flow in cylindrical pits is coupled to flow in the mainstream through the presence of a "trapped" vortex (or vortices) in the pit (Figure 1). For a pit of aspect ratio (=

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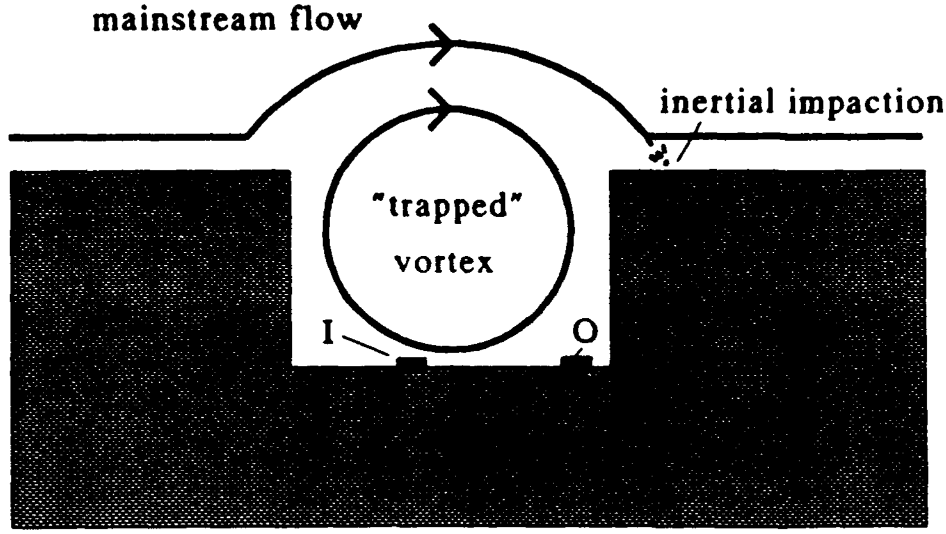

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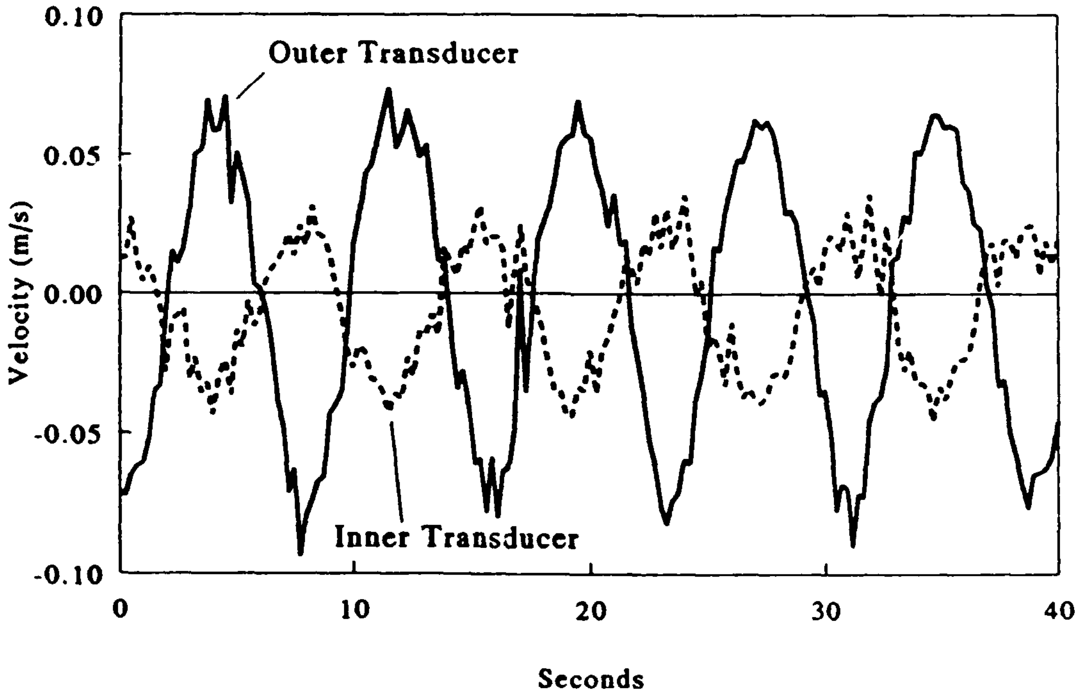

Figure 1: Flow in a pit microhabitat. (A) Boundary-layer flow along the substratum's surface produces a vortical flow in the pit. The vortex in turn affects the flow above the substratum, causing streamlines to move away from the substratum at the upstream edge of the pit and toward the substratum at the trailing edge. We hypothesize that it is this flow toward the substratum that enhances the deposition of spores and larvae near the pit edge. The labels "I" and "O" show the location of the inner and outer acoustic Doppler transducers, respectively. (B) The temporal variation in vertical velocity within the pit as recorded by the acoustic Doppler flowmeter. The flow oscillates in time with the mainstream. The inner transducer measures flow nearer the center of the trapped vortex and therefore shows a lower magnitude. Because the inner transducer is on the opposite side of center from the outer, the flow direction it measures is opposite that of the outer transducer.

depth/diameter) less than about 1, when the mainstream flow is to the right (as in this figure), the flow in the pit is characterized by a clockwise rotation. Thus the velocity at the bottom of the pit is in the opposite direction from that in the mainstream, an effect clearly seen in the flow visualization experiments. At higher aspect ratios, two counter-rotating vortices have been observed, and flow at the bottom of these pits is in the direction of the mainstream.

The maximal velocity in the trapped vortex is approximately 1/4 that in the mainstream. In this sense, a cylindrical pit can serve as a spatial refuge from mainstream hydrodynamic forces.

In oscillating flow, the direction of rotation of the "trapped" vortex changes as the direction of the mainstream flow changes. As a result, twice in each oscillatory cycle there are instants where the velocity in the microhabitat (as for flow over the exposed substratum) is zero. These periods of low or zero flow may provide a form of temporal refuge from hydrodynamic forces during which a swimming larvae may be able to actively affect its position relative to the substratum.

The exchange of water between the microhabitat and the mainstream is governed by both mainstream velocity and the aspect ratio of the pit. For a pit with low aspect ratio (diameter = depth = 6 mm), the volume in the pit is exchanged on average every 5 seconds, reaching a peak of once per second coinciding with a mainstream peak flow of 30 cm/s. Exchange in a higher-aspect-ratio pit (diameter = 3 mm, depth = 6 mm) is higher on

average (about 1 per second) and is characterized by sporadic bouts of very rapid exchange (up to approximately 20 volumes per second). The power spectrum of the volumetric exchange rate in pits closely matched those for mainstream velocity and wave height, indicating that pits reach a maximal exchange rate once per wave. This fact is somewhat surprising; one might expect one peak in the exchange rate on the inshore surge of a wave, and an equal peak on the offshore ebb. The observed asymmetry in exchange rate is explained by an asymmetry in the onshore-offshore velocity at the experimental site -- the peak inshore velocity was substantially higher than the peak offshore velocity, and therefore drove a faster exchange.

The peak exchange rate of one pit volume per second mentioned above for a low-aspect-ratio pit was measured under the same conditions in which a maximal rotational velocity of 7 cm/s was obtained. Because 1 rotation per second of a vortex 6 mm in diameter (the size of the pit) corresponds to a velocity of 1.8 cm/s, we conclude that water entrained into the "trapped" vortex is likely to make roughly 4 sweeps through a pit before exiting. Thus, the "trapped" vortex serves to retain entrained water and thereby may provide a mechanism by which larvae entrained into the microhabitat have repeated chances to settle on its walls.

Settlement Experiments

Plates placed in the field showed a distinct effect of pits in the substratum on the pattern settlement by algal spores, although not of a type we predicted. Very few spores settled

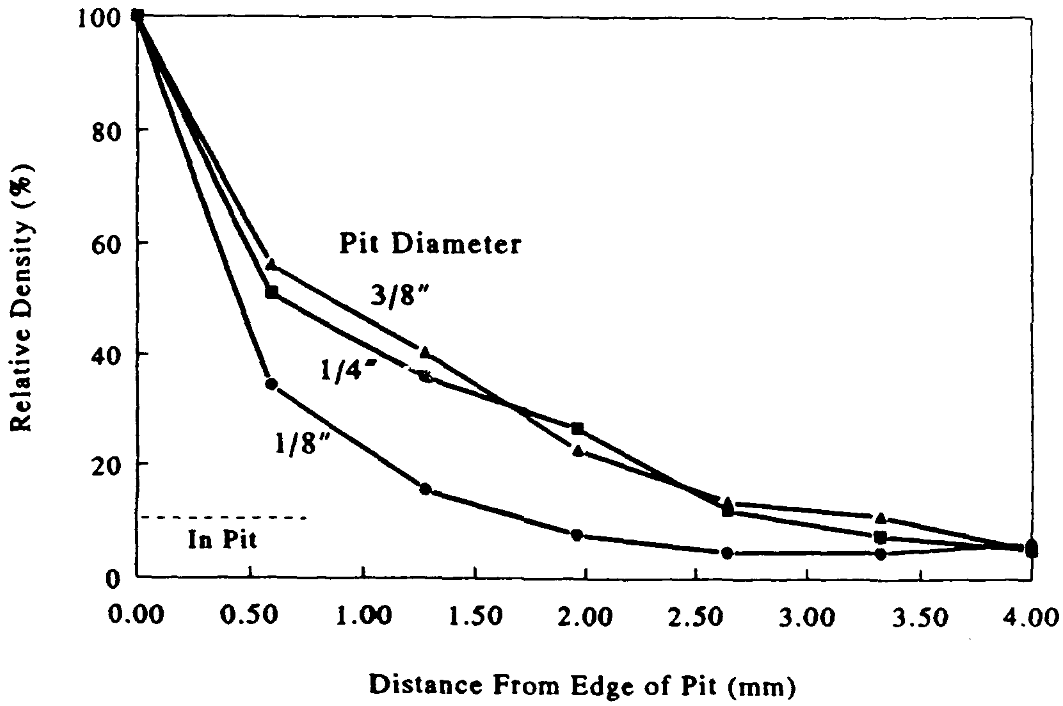

Figure 2: The pattern of settlement of algal spores on the substratum surrounding the openning of pits of various diameters. Settlement is most dense near the pit edge, decreasing in density with increasing distance from the edge. Settlement at the pit edge is much higher than settlement within the pit itself.

within the pits themselves, instead spores were found in a "halo" on the flat substratum surrounding each pit (Figure 2). The larger the hole, the more distinct the halo.

We believe that this "halo" effect can be explained by the presence of the "trapped" vortex in each pit. As the mainstream flow approaches a pit it is deflected upward by the vortical flow inside the pit. Flow is subsequently pulled back down toward the substratum at the trailing edge of the microhabitat (Figure 1). This substratum-directed flow induced by the "trapped" vortex seems likely to result in the inertial impaction of spores in the area adjacent to the downstream lip of the pit, resulting in turn in an enhanced deposition of spores. When the flow changes direction (as it does under surface waves) the area of high inertial-impaction rate switches to the opposite edge of the pit. Thus, areas both offshore and inshore of a pit are likely to exhibit an increased settlement rate, an effect that is evident in our data. An effect similar to this has been found for barnacle cyprid larvae by Butman & Mullineaux (1991). These results suggest that the most significant effect of flow in a microhabitat on an otherwise smooth substratum may be to influence the delivery of larvae and spores to areas outside the microhabitat itself.

The Tenacity of Algal Zygotes

The tenacity of Pelvetia zygotes increases with the time for which zygotes are in contact with the substratum, reflected in the fact that a smaller percentage of individuals are washed off

by a given shear stress as time increases (Figure 3). Even for short periods of time, however, a substantial fraction of zygotes is highly tenacious, suggesting that these organisms can effectively adhere under even extreme hydrodynamic conditions. For example, the velocity gradient next to the substratum in the experiment shown in Figure 3 was approximately 3000/s, yet at least 55% of zygotes settled on a clean surface remained attached. It thus seems unlikely that adhesion strength alone can limit the ability of these algae to settle.

CONCLUSIONS

As with many exploratory efforts, the project described here raises more questions than it answers. For example, we can now describe in some detail what the flow field is like in settlement microhabitats at a spatial and temporal scale appropriate to settling organisms. This information may be of considerable importance to biologists examining the post-settlement behavior and physiology of those organisms that show an active preference for these microhabitats. In terms of the hydrodynamic control of the pattern of delivery of larvae to the substratum, however, our results suggest that the principle effect of flow in a microhabitat is to affect the settlement of organisms <u>outside</u> of (but near) the microhabitat. Preference for the microhabitat itself is likely to be expressed through post-contact processes. For instance, barnacle larvae may be preferentially delivered to the substratum near the lip of a pit, whence they may actively move into the pit.

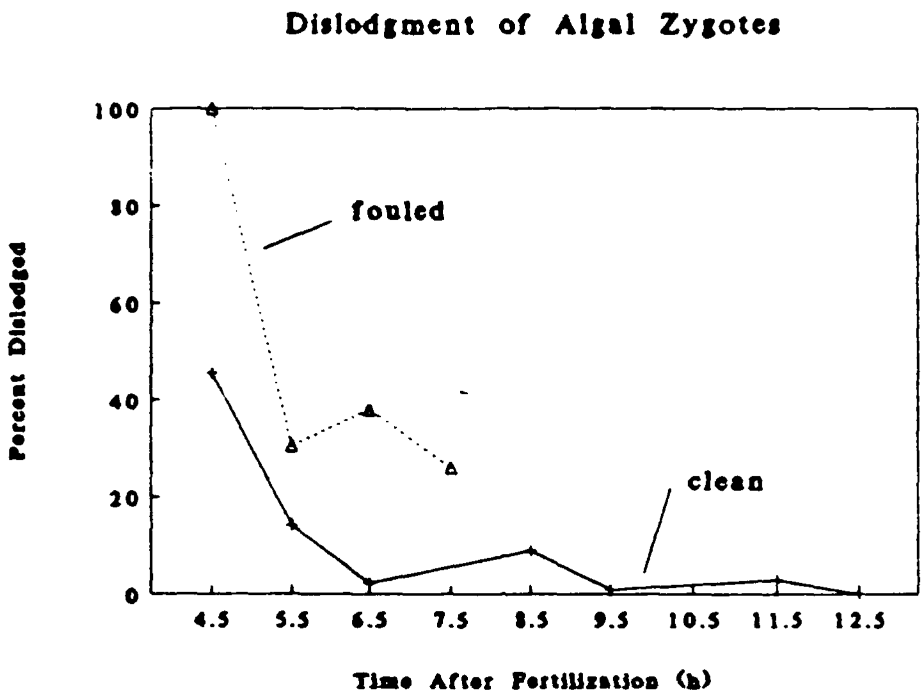

Figure 3: Proportions of *Pelvetia fastigiata* zygotes dislodged in flume experiments on both fouled and clean acrylic surfaces. Fouled plates were obtained by allowing panels to be naturally colonized in a flow-through aquarium. Flow conditions were laminar in the working sections with boundary shear stresses of 14.2 N/m^2, and maximal water velocity of 4 m/s at 1.4 mm above the surface. Data points represent means of 1 to 4 trials.

PUBLICATIONS

To date, the results of this project have been described in two publications:

Denny, M.W. & M.F. Shibata. 1989. Effects of surf zone turbulence on settlement and external fertilization. Am. Nat. 134:859-889.

Denny, M.W. & J.A.C. Humphrey. 1989. Fluid mechanical constraints on biotic functions. Mech. Eng. 111:50-53.

However, these publications pertain to only a fraction of the information gathered. The remaining data are currently being analyzed, and several additional manuscripts will be submitted for publication in the near future. These will of course be forwarded to ONR as they are published.

No patentable inventions were produced by this research.